

Rainforest Canopy Ants: The Implications of Territoriality and Predatory Behavior

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ABSTRACT

After first being ground-nesters and predators or scavengers, ants became arboreal with the rise of angiosperms and provided plants a biotic defense by foraging for prey on their foliage. Plants induce ants to patrol on their leaves through food rewards (e.g., extra-floral nectar and food bodies), while ants attend hemipterans for their honeydew. Most arboreal-nesting ants build their own nests, but myrmecophytes, plants that offer hollow structures that serve as nesting places to specialized “plant-ants”, illustrate the tight evolutionary bonds between ants and plants. In tree-crop plantations and in some rainforest canopies territorially-dominant arboreal ants have large colonies with large and/or polydomous nests. Their territories are defended both intra- and interspecifically, and are distributed in a mosaic pattern, creating what has become known as “arboreal ant mosaics”. They tolerate non-dominant species with smaller colonies on their territories. Arboreal ant mosaics are dynamic because ant nesting preferences differ depending on the species and the size and age of supporting trees. Because the canopy is discontinuous, arboreal-foraging ants can be found in ant mosaics; invasive ants can affect also the structure of the mosaic. We discuss here the methods that permit us to study these mosaics. Territorially-dominant arboreal ants are good predators that use group ambushing to catch flying insects on their host tree foliage. When producing winged sexuals they also forage for prey on the ground and plunder the colonies of non-dominant species sharing their host tree. When expanding their territories, the workers of the victorious colony raid the defeated colony. Because territorially-dominant arboreal ants prey on herbivores and strongly affect their general activity, ants are frequently used as biological control agents.

Keywords: ant mosaics, ant-plant mutualisms, myrmecophytes, predation, territoriality

Abbreviations: EFNS, extrafloral nectaries; FBs, food bodies; mya, million years ago

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INTRODUCTION

Within the insect order Hymenoptera, ants belong to the aculeate (i.e., having a stinging apparatus) sub-order and

represent the family Formicidae. The oldest known hymenopterans date from the Triassic Period (248-206 mya), and the oldest aculeate wasps from the Jurassic Period (206-144 mya). Ancestral ants diverged from the acu-

leate sub-order during the early Cretaceous Period (144-65 mya), most likely around 140 mya or even before since the oldest fossils date from ≈ 100 mya (Brady 2003; Dlussky and Rasnitsyn 2003; Nel *et al.* 2004; Moreau *et al.* 2006). Some subfamilies of ants began to diverge some 90 mya ago, but the rarity of ant fossils, compared to those of other insects, suggests that they were not particularly numerous between 80 and 60 mya (Grimaldi and Agosti 2001).

Contrarily, ants are relatively well represented in arboreal environments today, especially in intertropical countries. Despite extremely changeable daily climatic conditions, the scarcity of nesting sites and the unpredictable availability of prey in these exposed environments (Schulz and Wagner 2002), ants dominate the invertebrate communities in tropical rainforest canopies. Indeed, in these canopies, ants often represent 50% of the animal biomass and 90% of the individuals. This very high abundance, however, is coupled with only a moderate diversity in African (Dejean *et al.* 2000; Watt *et al.* 2002), American (Adis *et al.* 1984; Wilson 1987; Tobin 1994, 1995; Davidson and Patrell-Kim 1996; Davidson 1997), Asian (Stork 1991; Floren and Linsenmair 1997; Brühl *et al.* 1998) and Australian (Blüthgen *et al.* 2004) tropical rainforests. The high abundance of ants can be attributed to the fact that, independently of the area studied, most species are at least partially herbivorous, feeding on extrafloral nectar (EFN), food bodies (FBs), pollen, fungal spores and mycelium, epiphylls, sap, and as “cryptic herbivores” on hemipteran honeydew (Tobin 1994; Blüthgen *et al.* 2000; Dejean *et al.* 2000; Davidson *et al.* 2003; Hunt 2003; Blüthgen *et al.* 2004).

Yet, over a geological time-scale, ants were not always so present in arboreal environments and this adaptation to arboreal life, which is a noteworthy trait of evolution in the Formicidae, is certainly related to the arrival of angiosperms.

FROM GROUND-DWELLING TO ARBOREAL-DWELLING

Ant diversification closely tracks the rise of angiosperms between ≈ 100 mya and ≈ 50 mya (Fig. 1) and the ecological dominance of ants is notable by the mid-Eocene (50 mya) with already nearly all extant subfamilies and most genera in place, suggesting an explosive radiation just before this period (Wilson and Hölldobler 2005; Moreau *et al.* 2006). The proliferation of angiosperms is also known to have driven the diversification of major herbivorous insects, among them hemipterans with numerous taxa that developed relationships with ants (Grimaldi and Engel 2005).

Initially, ants were ground-dwelling predators or scavengers. Compared to the gymnosperms that previously dominated the flora, the arrival of angiosperms created more complex habitats on the ground and in the leaf-litter and their rise was accompanied by an increase in the abundance and diversity of potential prey, not to mention providing ants with the possibility of feeding on plant exudates (Grimaldi and Engel 2005; Wilson and Hölldobler 2005). Being a ground- or litter-dwelling predator or scavenger is, then, a plesiomorphic trait in ants; however, although the process of diversification was already well established by the mid-Eocene, most ant species had, like their Sphecomyrmecinae ancestors, circular or ovoid heads and short mandibles with small numbers of teeth (Wilson and Hölldobler 2005). As ants evolved, the morphology of the workers changed in two main ways: their heads changed shape and their mandibles became more elongated as they became specialized in predation, and their claws became more well-developed and bore adhesive pads permitting them to adopt an arboreal way of life (Hölldobler and Wilson 1990a; Federle *et al.* 2000; Orivel *et al.* 2001). For certain taxa, both of these types of changes occurred as the ants first became predators, and then became arboreal (Fig. 2).

Among the four major subfamilies (i.e., the Ponerinae, Myrmicinae, Formicinae and Dolichoderinae) characterized by their diversity, abundance and geographically wide-

spread distribution, the Ponerinae appeared first (Fig. 1). They were ground-dwelling, occupying the leaf-litter of forests, and as pre-eminent arthropod predators they flourished throughout the world (Wilson and Hölldobler 2005). Nevertheless, they remained primitive in their social organization: reproductive females and workers are similar in size (as opposed to other subfamilies where the queens are much larger than the workers, and have an hypertrophied thorax); the queens have a low level of fertility; their colonies are relatively small (generally several hundred individuals; this can be seen in the other subfamilies, but is exceptional) and are founded independently, but foundations must be repeatedly provisioned, thus exposing the queens to predators; most of the species have solitary foragers; and trophallactic exchanges remain exceptional (Peeters 1997). So, they were globally successful yet socially primitive, what Wilson and Hölldobler (2005) termed the “ponerine paradox”. This seems due to the causalities between solitary foraging and predation as a way of life that imply small colonies due to the relative paucity of prey (accentuated for species preying on particular arthropod taxa); the whole, in turn, renders other social traits simple and, hence, “primitive” (Wilson and Hölldobler 2005).

The Myrmicinae appeared second (Fig. 1); they were able to evolve by first occupying ground and leaf-litter sites and consequently by successfully competing with the Ponerinae. They therefore at least partially prevented the Formicinae and Dolichoderinae that appeared later from taking over these sites. Consequently, most Formicinae and Dolichoderinae species have relationships with plants (Fig. 1).

Based on current knowledge, the family Formicidae is extremely diverse with approximately 11,500 ant species known (Bolton *et al.* 2007) and an estimated 3,000 to 9,000 additional species as yet unknown to science. The phylogeny of the family is clearly separated into three clades divided into 19 subfamilies (14 of them are strongly monophyletic; three others are monotypic; and the remaining two, the Amblyoponinae and especially the Cerapachyinae, are paraphyletic) (Fig. 1; Moreau *et al.* 2006). It is worthy to note that 10 subfamilies are entirely composed of ground-dwelling predatory or scavenging ant species. These plesiomorphic traits, frequently found across the genera in the Ponerinae and the Myrmicinae, were less frequent among the Formicinae and rare in the Dolichoderinae (Fig. 1). In fact, many myrmecine, formicine and dolichoderine species are ground-nesting, but their workers forage mostly on plants to gather exudates or attend hemipterans. The same is true for the less diverse subfamilies (i.e., the Paraponerinae, Myrmecinae, Heteroponerinae and Ectatomminae) with *Paraponera clavata* and *Ectatomma tuberculatum* building their nests at the base of the large trees on which they forage (Tillberg and Breed 2004). Finally, the very abundant canopy ants, here also mostly myrmecine, formicine and dolichoderine species, represent a large proportion of the overall animal biomass in this habitat where the irregular availability of prey means that they are omnivorous.

Ground-nesting, foliage-foraging species probably constitute the first line of defense in the plants' biotic protection thanks to their predatory activity (Dejean *et al.* 2006). Indeed, defoliating insects have frequently developed means of resisting plants' chemical defenses, but they rarely possess successful counter-adaptations against ants (Coley and Kursar 1996). Some lineages of ants developed tight evolutionary bonds with plants and became arboreal-nesting and foraging. Ant-plant interactions vary from facultative “diffuse” relationships to obligatory “specific” associations. In diffuse relationships plants induce different ant species to patrol their foliage by producing energy-rich food rewards such as EFN and/or FBs. However, the myrmecophyte-ant association is strict and necessary to the survival of both partners, with myrmecophytes offering a nesting place (i.e., hollow structures called domatia) and frequently EFNs or FBs to specialized “plant-ants”. In return, the latter protect the myrmecophytes from a broad range of herbivores plus competitors and fungal pathogens, and/or provide them

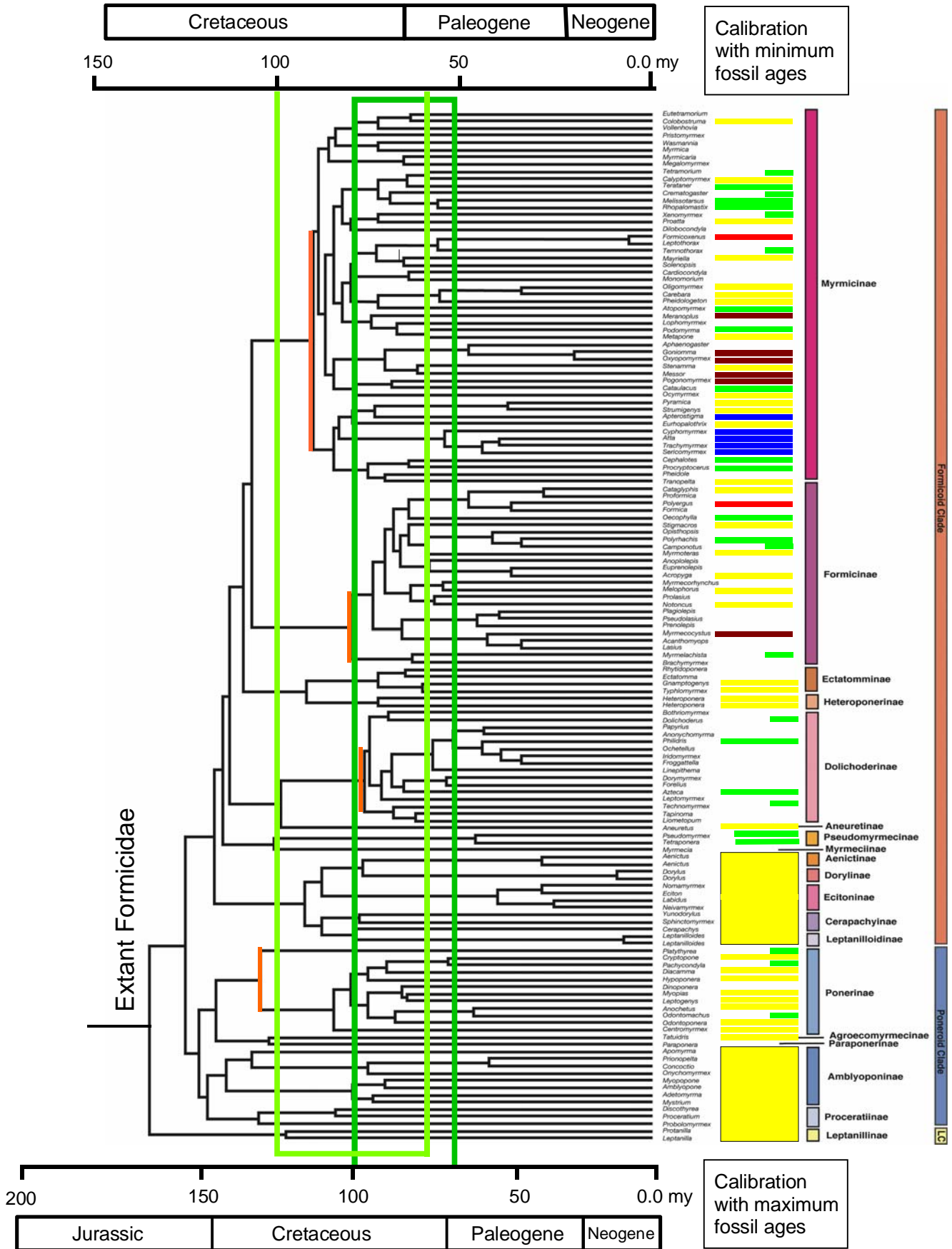


Fig. 1 Phylogenetic chronogram of ants, modified based on Moreau *et al.* (2006). Green lines delineate the rise of angiosperms depending on whether minimum or maximum ages are used for fossil calibrations (respective time scales are indicated in plots situated above and below topology). The vertical red lines show when Ponerinae, Myrmicinae, Formicinae and Dolichoderinae appeared. Yellow rectangles correspond to the 10 subfamilies composed only of ground-dwelling, predatory or scavenger species (Heteroponerinae are not included here because *Acanthoponera*, not represented in the figure, are ground-nesting arboreal-foraging species). The same is true for the yellow lines, but at the genus level (includes termite predators living in the walls of the termitaries). Green lines correspond to genera entirely (or almost entirely) composed of arboreal species; short green lines to genera with some arboreal ant species. Blue lines correspond to genera composed of fungus-growing species and brown lines to genera entirely composed of granivorous species. Red lines correspond to genera entirely composed of parasitic or slave-making ant species. Species belonging to the other genera, mostly ground-nesting, have diffuse relationships with plants, exploiting exudates. Certain genera, such as *Acropyga* include species that attend hemipterans underground.



Fig. 2 A *Daceton armigerum* worker capturing a locust. This arboreal-dwelling myrmecine species belongs to the tribe Dacetini whose other species are ground-dwellers specialized in collembolan predation. Note the heart-shaped head and the hypertrophied trap-jaw mandibles.

with nutrients (Beattie and Hughes 2002; Heil and McKey 2003). For example, in the association between Central American *Acacia* spp. and ants of the genus *Pseudomyrmex*, the plants provide ants with EFN and protein-rich FBs, while the ants protect the host-tree foliage from herbivorous insects and mammals through their territorial aggressiveness (they do not hunt). They also kill neighboring trees and encroaching vines by stinging them, preventing their host *Acacia* from being overwhelmed. Myrmecotrophy, or the ability of certain plants to absorb nutrients from the refuse of their associated ants, has mostly been demonstrated for epiphytes. Yet, this adaptation to live in nutrient-poor environments has also been noted for several geophytic myrmecophytes (Rico-Gray and Oliveira 2007). Although most myrmecophytic species need sunlight (but some can develop in the understory), they are mostly found in pioneer formations and only a few, such as *Tachigali* spp. and *Cecropia* spp. in the Neotropics and *Barteria fistulosa* in Africa, can be found in rainforests where they are able to reach the canopy (Fonseca and Benson 2003; Davidson 2005a; Dejean *et al.* 2007a).

THE NOTION OF AN ANT MOSAIC

Wilson (1958) first noted that the arboreal ant fauna in tropical rainforests had a patchy distribution, but the notion of an “ant mosaic” appeared later in a series of studies conducted in African cocoa tree plantations (Room 1971; Majer 1972; Leston 1973; Majer 1976a, 1976b; Taylor 1977; Jackson 1984b). Cocoa plantations provide an easily attainable “canopy” that allows for the rapid and efficient identification of the ant species occupying each individual tree. The concept of “ant mosaic” was later generalized to include American, Asian, Papuan and Australian forests, as well as tree crop plantations (Room 1975; Leston 1978; Winder 1978; Majer 1990, 1993; Paulson and Akre 1991; Adams 1994; Andersen and Reichel 1994; Majer *et al.* 1994; Andersen 1995; Medeiros *et al.* 1995; Dejean *et al.* 1999; Ambrecht *et al.* 2001; Blüthgen and Stork 2007; Pfeiffer 2007).

These studies have shown that the canopies of tropical forests and tree crop plantations are occupied by “territorially-dominant” species, or those ant species that defend space *per se* (i.e., absolute spatial territories), usually from both intra- and some interspecific enemies (Davidson 1998). They are characterized by: (1) extremely populous colonies (several hundred thousand to several million individuals), (2) the ability to build large and/or polydomous nests (carton builders, carpenter ants and weaver ants; **Fig. 3**), and particularly (3) a highly developed intra- as well as inter-specific territoriality that causes their territories to be distributed in a mosaic pattern in the forest canopies (Leston 1973). Hölldobler and Lumsden (1980) showed, for instance, that territorially-dominant species such as *Oecophylla* gain a considerable advantage by excluding conspecific aliens and other dominant ant species from their “absolute territory” rather than only from their nests and food resources. Such territories are defended 24/7, especially at the peripheries, leading to the formation of unoccupied zones or “no ants’ lands” (Hölldobler 1979; Hölldobler and Wilson 1978, 1990a). Also, these territories are marked with persistent landmarks that can last for more than one year (Dejean and Beugnon 1991; Beugnon and Dejean 1992) and are recognized by other ants that avoid them or adapt their behavior so as to avoid encountering the occupying ants (Dejean *et al.* 2005; Offenberg 2007).

The zones to be defended are therefore limited to an area within definite boundaries and to “no-ants’ lands” bearing particularly dense landmarks (visible to humans as they are brownish anal spots containing true territorial phero-

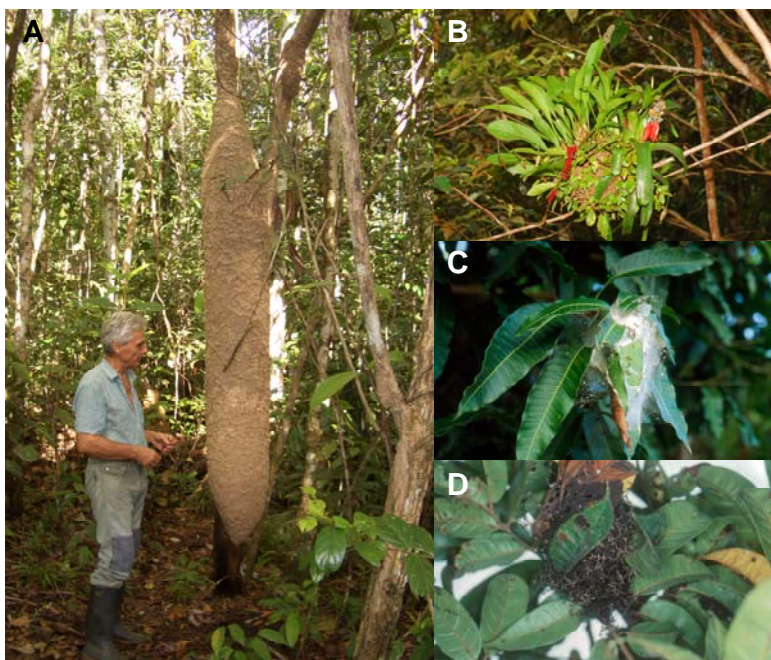


Fig. 3 Different nest of territorially-dominant arboreal ant species. (A) Large carton nest of *Azteca charitex* in French Guiana. (B) An ant garden of the parabioc species *Camponotus femoratus* and *Crematogaster levior*, also in French Guiana. The ants plant epiphyte seeds in the carton of their nest, then shelter between the roots of the epiphytes. (C) In Cameroon, a nest of *Oecophylla longinoda* that workers built by binding together leaves of the supporting tree using the silk of their larvae. (D) Also in Cameroon, a nest of *Tetramorium aculeatum* built between the leaves of the supporting tree, this time using carton.



Fig. 4 After a battle a *Tetramorium aculeatum* worker is still biting one antenna of an *Oecophylla longinoda* major worker.

mones) that separate them from neighboring colonies so that encounters with alien workers are infrequent (Hölldobler and Wilson 1990a [p. 287]; Offenberg 2007). Fighting nevertheless does occur when growing colonies expand their territory (Fig. 4; Jackson 1984a). After the experimental elimination of a dominant colony through the use of insecticides, neighboring colonies rapidly expanded their territories (Majer 1976a), providing evidence for territorial conflicts between neighboring colonies.

Certain ant species can defend absolute territories because energy is not a limiting factor as these species exploit sugar-rich EFN and especially the honeydew produced by hemipterans (Davidson 1997; Blüthgen *et al.* 2000; Dejean *et al.* 2000; Hossaert-McKey *et al.* 2001; Davidson *et al.* 2003; Blüthgen *et al.* 2004). The defining role of hemipterans can be illustrated by the absence of an ant mosaic in the lower canopy trees of a pristine forest in Borneo where ant-attended hemipterans were largely absent (Floren and Linsenmair 2000), while ant mosaics exist in the upper canopy in the same bio-geographical region (Blüthgen and Stork 2007).

In ground-dwelling species, one can distinguish between “numerical dominance” or the predominance of a species in number, biomass and/or frequency of occurrence in the ant community; “behavioral dominance” or dominance in interspecific competition due to superior fighting and/or recruitment abilities; and “ecological dominance” that applies to invasive species, or the combination of both numerical and behavioral dominance (Davidson 1998).

TERRITORIALLY-DOMINANT ARBOREAL ANTS' RELATIONSHIPS WITH OTHER ANTS

Territorially-dominant arboreal ants tolerate on their territory the presence of “non-dominant” species having relatively small colonies (up to a few thousand individuals) and generally nest in pre-existing botanical structures (e.g., hollow branches, rough bark, epiphytes). When large *Oecophylla longinoda* colonies develop sexual brood, the need for protein is so great that workers rob the prey or even attack and plunder the brood of non-dominant species (Hölldobler and Wilson 1990a [p. 429]; Majer *et al.* 1994; Mercier *et al.* 1998; Dejean and Corbara 2003).

An intermediary status, known as “sub-dominant”, corresponds to species that generally act as non-dominants but which are able, under certain conditions, to defend territories in the same way as do dominants (Majer 1972, 1993; Leston 1973; Hölldobler and Wilson 1977, 1978; Hölldobler 1979, 1983; Majer *et al.* 1994). A colony of a non-dominant species reaches the status of sub-dominant when it is able to occupy an entire tree crown and exclude neighboring dominant species from its trees (plantations: Majer 1976a, 1976b; mangrove: Dejean *et al.* 2003).

Two species sharing the same territory and that behave as dominant were called “co-dominant” by Majer (1976b). This phenomenon is frequently the result of the complementary rhythm of activity of the two species, one being diurnal the other nocturnal (Mercier and Dejean 1996; Dejean and Olmsted 1997; Mercier *et al.* 1997, 1998; Hossaert-McKey *et al.* 2001). Co-dominance is often missed by researchers who, by working during the day, can overlook the presence of nocturnal species, regardless of the sampling technique used. This is the case for *Paraponera clavata*, a nocturnal Neotropical species that nests in the ground at the base of extrafloral nectary-bearing trees. During the day, the trees can appear devoid of ants or be occupied by *Crematogaster* spp., while, at night, numerous giant workers of this species forage in the foliage (Young and Hermann 1980; Breed and Harrison 1989; Hölldobler and Wilson 1990b).

Despite being a territorially-dominant arboreal ant species, *Oecophylla smaragdina* can share trees with *Crematogaster fusca* in Australia (in this case they are co-dominant), but never with *Anonychomyrma gilberti*, the third dominant species recorded in the area studied by Blüthgen and Stork (2007).

It seems that co-dominance is frequent in the Neotropics. By using the canopy raft to reach the canopy of a forest in French Guiana, for example, we were able to verify that each of the five most frequent numerically dominant species can share a tree with another one (Dejean *et al.* 1999). In this case, the foraging workers of the two co-dominant species forage on the same branches at the same time. An ant mosaic still exists, but this time each association constitutes a “territorially-dominant entity”. Parabolic species that share both nests and trails represent the most extreme example of co-dominance. They are frequent, particularly *Camponotus femoratus* and *Crematogaster levior* (Davidson 1988; Orivel *et al.* 1997).

CHARACTERISTICS OF TERRITORIALLY-DOMINANT ARBOREAL ANTS

General traits

The typical characteristics of territorially-dominant arboreal ants can be summarized in five traits. (1) Their intra- and inter-specific territoriality (Leston 1973) is associated with (2) the relatively large size of their colonies (but numerically abundant species are not necessarily territorial; Davidson 1998) and with, in most cases, polydomous nests that permit the colonies to easily access permanent food sources (Hölldobler and Wilson 1990a), especially (3) the sugar-rich honeydew of hemipterans needed to fuel energy-costly territoriality (Blüthgen *et al.* 2000, 2004; Dejean *et al.* 2000; Davidson *et al.* 2003, 2004; Davidson 2005b). This is associated with (4) a modified proventriculus enabling workers to effectively harvest the honeydew (Davidson 1997; Davidson *et al.* 2004), (5) a thin cuticle and non-proteinaceous venom limiting the need for nitrogen (Davidson 1997; Orivel and Dejean 1999) and (6) efficacious alarm pheromones (Dejean 1990a; Hölldobler and Wilson 1990a; Djiéto-Lordon *et al.* 2001; Richard *et al.* 2001). Ant species corresponding to these criteria belong mostly to the genera *Azteca* (Neotropics), *Camponotus*, *Crematogaster*, *Dolichoderus* (worldwide), and *Oecophylla* (Paleotropics) (Majer 1993; Adams 1994; Davidson 1997).

Note that most, if not all, of these traits, particularly territoriality, exist in plant-ants associated with myrmecophyte species that are able to grow up to the canopy (Davidson 2005a; Dejean *et al.* 2007a, 2007b).

Trophobiosis

Trophobiosis with hemipterans seems primordial for territorially-dominant arboreal ants. Compared with EFNs, the hemipterans' spatial distribution is generally more concentrated, and individuals can be transported by the workers

from one place to another, more adequate site (Hölldobler and Wilson 1990a; Blüthgen *et al.* 2004). Floren and Linsenmair (2000) noted the absence of ant mosaics in the lower canopy trees in a mature forest in Borneo, something that Blüthgen and Stork (2007) suspected was due to the rarity of hemipterans in this shady area. The same was found to be true in an Australian forest formation (Majer and Camer-Pesci 1991). In fact, extrafloral nectaries and honeydew-producing insects shape the species distribution of dominant ants (Blüthgen *et al.* 2000; Dejean *et al.* 2000; Hossaert-McKey *et al.* 2001; Blüthgen *et al.* 2004).

Predatory behavior

Although these ants feed extensively through trophobiotic associations with hemipterans whose honeydew contains a large proportion of their nitrogen requirements (Blüthgen *et al.* 2003; Davidson *et al.* 2003) and although they prey on some of their attended trophobionts (Way 1963; Hölldobler and Wilson 1990a [p. 527]; Delabie 2001), most of them are very good predators. This was shown indirectly through ^{15}N analyses (Davidson *et al.* 2003), and directly through field studies, including those conducted in the forest canopy (Floren *et al.* 2002; see also Dyer 2002) or in plantations (Philpott and Armbrrecht 2006).

The predatory behavior of the weaver ant, *Oecophylla longinoda*, the first species studied in this context, is adapted to the fact that in a tree's foliage most prey are likely to escape by flying or jumping away or by dropping. Workers hunt diurnally in groups. Prey detected visually from a relatively long distance are seized by an appendage and immobilized by a first worker that then releases a pheromone to attract nestmates. Recruited nestmates, in turn, seize a prey appendage and pull backward, spread-eagling the prey. This behavior, which is used even for relatively small prey, also permits the ants to capture large insects and even other animals (Dejean 1990a, 1990b; Hölldobler and Wilson 1990a). Entire prey are retrieved cooperatively, including, in some cases, heavy prey such as small birds (Fig. 5; Wojtusiak *et al.* 1995). This form of prey capture and



Fig. 5 An *Oecophylla longinoda* worker is able to hold onto a small bird alone while its nestmates recruit other workers at long range, illustrating the power of the worker's claws and adhesive pads.



Fig. 6 *Crematogaster gabonensis* hunting an army ant *Dorylus nigricans* soldier (in Cameroon) on the ground. (A) A first worker discovers the *Dorylus* soldier and, emitting an alarm pheromone, begins to recruit nestmates. (B) Several recruited workers arrive and begin to bite the soldier. (C) The soldier is spread-eagled by numerous *Crematogaster gabonensis* workers.

retrieval requires that the workers adhere to the substrate by means of very powerful adhesive pads and claws, a characteristic that seems general in arboreal species (Wojtusiak *et al.* 1995; Federle *et al.* 2000; Djiéto-Lordon *et al.* 2001; Orivel *et al.* 2001; Richard *et al.* 2001).

Other dominant ants exhibit a relatively similar behavior based on the spread-eagling of the prey. Detection may occur from a short distance or even by contact; venom is generally used to subdue the prey prior to cutting it up and transporting it in small pieces. This concerns African Myrmicinae *Atopomyrmex mocquerisii*, *Crematogaster* sp. and *Tetramorium aculeatum* (Djiéto-Lordon *et al.* 2001; Richard *et al.* 2001), and the Neotropical Dolichoderinae *Azteca chartifex* (Rousson 2002).

We saw above that territorially-dominant arboreal ants can prey on non-dominant species or on their enemies. When colonies of *Oecophylla* spp., *Crematogaster* spp. and

Azteca from the *chartifex* group become large and produce sexual brood they also hunt on the ground. Consequently, they are frequently recorded in samples of ground-dwelling ants (Deblauwe and Dekoninck 2007; see also McGlynn 2006 for Neotropical species). *Oecophylla longinoda* workers that forage on the ground around the base of their host trees, defend prey-rich secondary territories (Dejean 1990b; Hölldobler and Wilson 1990a [p. 401]; Dejean 1991), or can even organize expeditions very similar to those of army ants (Ledoux 1950; Dejean unpublished data). They particularly prey on *Dorylus* workers when a column passes close to the base of their host tree (Godwald 1972; Dejean 1991); the same is true of territorially-dominant arboreal *Crematogaster* (Fig. 6).

Territorially-dominant arboreal ants as omnivores

Because they can both hunt and engage in trophobiosis, should we consider territorially arboreal ant to be good predators, cryptic herbivores, or omnivores? Indeed, most dominant ants hunt to feed their larvae, particularly sexual brood that need protein so that their wing muscles can develop. Consequently, the diet of an ant colony may change seasonally and workers become more predatory when the colonies produce larvae destined to become winged sexuals. Also, for many species, queens lose their wings just after swarming and found their colonies claustrally. They then feed their first larvae with the histolysis of their wing muscles, showing the importance of protein in the development of ant larvae. On the contrary, in arboreal ant species the workers' diet is mostly composed of carbohydrates due to their need for energy (Hölldobler and Wilson 1990a). Depending on the species, larvae are able to feed directly on the prey that has been brought back to the nest by the workers; if not they imbibe the haemolymph or lick small pieces of prey that the workers offer to them. The size of a worker's oesophagus, several dozen micrometers in diameter, does not permit ants to swallow solid food, implying that workers and queens consume only liquids, with the queens being mostly fed through trophallaxis or being given trophic eggs (Hölldobler and Wilson 1990a; Davidson *et al.* 2004; Passera and Aron 2005). As a result, predation is a means by which worker ants gather food mostly for the larva in their colonies.

FACTORS INFLUENCING THE DISTRIBUTION OF TERRITORIALLY-DOMINANT ARBOREAL ANTS

Habitat selection by dominant ants

Several authors have evoked the microhabitat preferences of several territorially-dominant ant species; for instance, in West Africa *Crematogaster stadelmanni* and *Tetramorium aculeatum* are relatively shade-tolerant if compared to *Oecophylla longinoda* that preferentially nest in sunny areas (Majer 1976c), much like *Oecophylla smaragdina* does in Australia (Majer and Camer-Pesci 1991). The age of the plantations (from young trees to mature, fruit-producing individuals) (Majer and Camer-Pesci 1991; Bigger 1993) or of vegetal formations (from pioneer formations to secondary, and then mature forests) also plays a role (Floren *et al.* 2001; Schultz and Wagner 2002; Watt *et al.* 2002; Floren and Linsenmair 2005; Dejean *et al.* 2007a). Ground-nesting, plant-foraging species can defend territories at least while the trees are not too high. *Crematogaster striatula*, for example, is frequent in cocoa tree plantations and along forest edges in West Africa (Leston 1973; Dejean and Gibernau 2000).

In tree crop plantations, the proportions of the different dominant ants vary with the cultivated tree species. *Oecophylla longinoda* and *O. smaragdina* are relatively frequent on citrus and mango trees, less frequent on cocoa trees plantations, and rare on palm trees (Majer 1976a, 1976b; Jackson 1984b; Dejean *et al.* 1997; Mercier *et al.* 1997; Way and Bolton 1997; Kenne *et al.* 2003). Selective plant

attractiveness has been demonstrated during ethological studies on *Oecophylla longinoda* and *Tetramorium aculeatum*, two species that compete for nesting sites in West Africa. The selection of host plants by winged females (dissemination of colonies) and workers (colony budding) can take either of two paths. *Oecophylla* individuals spontaneously select the leaves of citrus or mango trees rather than the leaves of cocoa and guava trees, the contrary being true for *Tetramorium* workers. An imprinting process, which can supersede "innate" attraction, also exists. Individuals bred in contact with one of the tested plants during larval life (pre-imaginal learning) or the first days of adult life (early learning), or both, have a tendency to choose leaves of the plant species with which they were bred in contact. After several days of adult life, this conditioning is impossible, showing the existence of a "sensitive period" after which the influence of the environment ceases (Djiéto-Lordon and Dejean 1999a).

The impact of invasive ant species on ant mosaics

Of the approximately 11,500 ant species known (Bolton *et al.* 2007), about 150 so-called "tramp species" have been transported and introduced into many parts of the world through human activity, but only some have become invasive (Holway *et al.* 2002). Invasive ants form large supercolonies through their ability to achieve "unicoloniality" and resulting in the absence of intraspecific territoriality over extremely extensive areas. Large colony sizes and the absence of aggressiveness between workers are possible thanks to particular modes of reproduction, including clonal reproduction* (Fournier *et al.* 2005), meaning that workers are closely genetically related (Tsuji and Yamauchi 1994; Tsutui *et al.* 2003; Pedersen *et al.* 2006). Furthermore, the formation and success of supercolonies is facilitated by (1) being away from co-evolved parasites, predators and competitors (or the "enemy release" hypothesis), (2) the possibility of attending native as well as introduced hemipterans (once again, one can note here the importance of hemipterans on a large scale, and (3) a high level of aggressiveness towards native ants, that are displaced or eliminated most likely through a combination of predation and competition (Holway *et al.* 2002; Le Breton *et al.* 2005). Indeed, we saw above that "ecological dominance", or the combination of both numerical and behavioral dominance, applies to invasive ant species (Davidson 1998).

Invasions by alien ant species trigger the dismantling of native ant communities as has been demonstrated in northern California where native ant communities exhibit significant species segregation consistent with competitive dynamics. On the contrary, in areas invaded by the Argentine ant the communities of native ant species appear to be random or only weakly aggregated. The shift from a structured to a random community is rapid, occurring within a year of invasion (Sanders *et al.* 2003; see also Gotelli and Arnett 2000 concerning *Solenopsis invicta*). Consequently, because invasive ant species not only reduce biodiversity in general but rapidly disassemble ant communities, they strongly alter community organization among those species that survive their invasion. We therefore expect ant mosaics to be disrupted in areas taken over by an alien invasive ant (Fisher *et al.* pers. comm.).

Potentially invasive ant species do not always adversely

* In ants, as in other Hymenoptera, males are haploid, produced from unfertilized eggs and so have only one copy of each gene; while fertilized eggs become diploid females with two copies (Haplodiploidy). Females differentiate into gynes, or the future reproductive queens, and non-reproductive workers. The latter pass on their genes through "kin selection" (rearing relatives with whom they share genes). In the little fire ant *Wasmannia auropunctata* the gynes are identical to the reproducing queens. The workers are produced sexually, but because they are sterile the males are excluded as evolutionary actors. Also, they are produced clonally through a process not yet entirely elucidated, but it is likely that they result from the elimination of the maternal genome after fertilization.

alter the ecosystem and can act like territorially-dominant species within ant mosaics. For example, the Neotropical species *Wasmannia auropunctata*, considered to be one of the most destructive of the invasive ant species (Holway *et al.* 2002; Le Breton *et al.* 2005), has been identified as a territorially-dominant ant in Brazilian cocoa farms (Majer *et al.* 1994). This species reproduces clonally both in areas where it has been introduced and in disturbed areas of its native range, whereas it reproduces sexually in undisturbed areas of its native range (Fournier *et al.* 2005; Le Breton *et al.* 2006; Orivel pers. comm.).

The existence of an ant mosaic was also demonstrated in Bornean and Malaysian oil palm tree plantations (Pfeiffer *et al.* 2007) although the invasive ant *Technomyrmex albipes* was by far the most frequent species noted in both areas (along with two other, less frequent invasive ants). In Papua New Guinea, *Technomyrmex albipes* was found in ant mosaics on cocoa plantations (Room 1975) and in old secondary forests (Missa *et al.* 1998). *Technomyrmex albipes* is widespread throughout the islands of the Indian Ocean, the Indo-Australian region and the Pacific Ocean (Wilson and Taylor 1967). The reproductive castes include ergatoid females and males in addition to alates of both sexes, favoring the formation of supercolonies (Tsuji and Yamauchi 1994). But unlike most other invasive ants, the success of *Technomyrmex albipes* is not associated with a high level of aggressiveness, explaining why it can share its territories with several non-dominant ant species (Way *et al.* 1989; Pfeiffer *et al.* 2007). Nevertheless, numerical advantage, combined with the ability to mass recruit nestmates, permits workers of this species to rapidly deplete food sources, eliminating native species through exploitation competition (Warner *et al.* 2005). It is probable that in this palm tree plantation the territoriality of the dominant, native species, particularly the oft-studied *Oecophylla smaragdina* and *Pheidologeton affinis*, play a determinant role in shaping the ant community, and in preserving a mosaic structure.

Height of the vegetal formations, space between trees and savanna ants

It might seem unnecessary to reiterate that ant mosaics are to be expected among territorially-dominant **arboreal** species (with eventually rare cases of sub-dominant species). Nevertheless, certain ground-nesting, plant-foraging ant species that are more typical of the savanna can be registered during sampling in tree crop plantations. *Camponotus acvapimensis* and *Myrmecaria opaciventris*, two species frequent in the West African savanna (Taylor 2006), were, for example, registered in cocoa, guava, citrus and mango tree plantations (Majer 1976a, 1976b; Kenne *et al.* 2003). This is particularly the case in young plantations with relatively small trees whose crowns are not in contact with each other, a characteristic shared with savannas where trees are sufficiently small and/or widely spaced. As the plantations grow older arboreal ants take over little by little (Majer and Camer-Pesci 1991; Bigger 1993). The same is true for pioneer trees as they get older (Dejean *et al.* 2007a). Also, in plantations of trees with low canopies (e.g., guava, citrus and certain varieties of mango trees), ground-nesting, plant-foraging species dominate during periods when the plantations are being treated with insecticides; they are replaced by arboreal ant species when the treatment ceases (Kenne *et al.* 2003). Along forest edges ground-nesting, plant-foraging species, mostly savanna species, are frequent and probably flourish in that situation, as the ground is exposed to sunlight and EFN-producing lianas and pioneer trees are numerous (Dejean *et al.* 1994; Dejean and Gibernau 2000).

Even though the workers of different ground-nesting, plant-foraging species belonging to large colonies can be noted on the same trees (see Majer and Camer-Pesci 1991) a segregation probably exists related to a kind of territoriality as the workers of different species can occupy the same tree crowns, but one species is more frequent than the others (Kenne *et al.* 2003). Nevertheless, they do not defend

absolute territories and, as such, calling their distribution an "ant mosaic" is excessive. When their colonies reach a certain size some ground-nesting, plant-foraging species are more successful in defending territories against territorially-dominant ants than others. This is the case in West Africa for *Crematogaster striatula* that was registered in numerous studies concerning plantations of trees with low canopies (Room 1971; Leston 1973; Majer 1976a, 1976b; Jackson 1984a, 1984b; Kenne *et al.* 2003) and low vegetal formations along forest edges (Dejean *et al.* 1994; Dejean and Gibernau 2000). Nevertheless this species is supplanted by arboreal ants when the vegetal formations grow higher (Dejean *et al.* 2007a). We saw above that in the Neotropics *Ectatomma tuberculatum* and *Paraponera clavata* nest in the ground at the base of trees and can occupy an entire crown. Nevertheless, *Ectatomma tuberculatum* workers, that forage 24/7, are pressured by nocturnal *Crematogaster* spp. workers that rob from them the nectar that they have retrieved (Wheeler 1986; Richard *et al.* 2004). *Paraponera clavata* is rather a co-dominant species foraging mostly nocturnally on trees that are frequently occupied by *Crematogaster* spp. during the day (Young and Hermann 1980). Note that workers of both species forage solitarily (Young and Hermann 1980; Dejean and Lachaud 1992), whereas territorially-dominant arboreal ants hunt in a group.

The space between trees and pressure from ground-nesting, plant-foraging species that are already present and that tend to remain in the same area can be factors in keeping arboreal ant colonies from nesting in plantations (see Dejean *et al.* 2007a). This was true in Northern Australia both for tree crop plantations and natural vegetal formations where "ant mosaics" were not noted although a territorially-dominant species, *Oecophylla smaragdina*, was present. Here again a ground-nesting, plant-foraging savanna ant, *Opisthopsis haddoni*, was very frequent (Majer and Camer-Pesci 1991). In this situation, colonies of arboreal ant species make paths on the ground between trees (an *Oecophylla longinoda* queen can, for example, move from one tree to another; Fig. 7) that they need to keep open as the colony grows so that we registered a kind of colony budding when the path is not kept up continually (unpublished data). In a Cameroonian oil palm plantation where the canopy of the trees is relatively high (10-16 m in height) if compared to cocoa or guava trees and far apart enough so that their crowns are isolated from each other in most cases, two territorially-dominant arboreal ant species, *Crematogaster gabonensis* and *Tetramorium aculeatum* dominated, but *Paratrechina longicornis* and *Pheidole megacephala*, mostly ground-nesting species were also recorded (Dejean *et al.* 1997). A relatively similar situation was noted in oil palm tree plantations in Borneo and Malaysia, with *Oecophylla smaragdina* (a territorially-dominant arboreal species) and *Technomyrmex albipes* (an invasive species) being the most frequent (Pfeiffer *et al.* 2007).



Fig. 7 Major workers watch over the moving of an *Oecophylla longinoda* queen.

Size of the tree crowns and shape of the canopy

Although they can grow to be very tall and have wide trunks, a frequent feature among trees in French Guiana is a relatively small crown and a relative variation in tree height meaning that several trees can be found in the same surface unit. As a consequence the tree crowns are rarely in contact or interconnected by lianas, so that the area available to territorially-dominant arboreal ants is frequently limited. Consequently, although territorially-dominant arboreal ants exist (Adams 1994), their territories are not necessarily in contact so that the notion of an ant mosaic might be more a result of the canopy structure rather than due to ant territoriality or competition (Dejean *et al.* 1999). Also, certain trees are not occupied by a dominant ant species or by a pair of co-dominant species.

EXPANSION OF TERRITORIES BY TERRITORIALLY-DOMINANT ARBOREAL ANTS

During conflicts between neighboring territorially-dominant species, territoriality and predation seem to be related. For instance, Hölldobler (1983) noted that after combats with neighboring ants, *Oecophylla* spp. workers retrieved killed enemy workers as prey (see also Hölldobler and Wilson 1990a; p. 415). We observed the same phenomenon in Cameroon after a combat took place between *Oecophylla longinoda* and *Tetramorium aculeatum*. *Oecophylla longinoda* even organized raids on colonies of the plant-ant *Tetraponera aethiops*, and then occupied the foliage of their host plant (the myrmecophyte *Barteria fistulosa*). This explains why some *Barteria fistulosa* were occupied by *Oecophylla longinoda* during a recent study (Dejean *et al.* 2007a; see also Djiéto-Lordon *et al.* 2004). Furthermore, when colonies of *Polyrhachis laboriosa* reach a relatively large size, they can occupy an entire tree crown, and, thus, acquire the status of sub-dominant. In this case, workers individually hunt the workers of neighboring species, particularly *Crematogaster stadelmanni*, triggering a kind of panic among the latter (unpublished data).

Researchers who work frequently in the field can note that territorial expansion does not occur progressively. During very long periods (several months or even years) without conflict, the workers of each neighboring colony avoid venturing onto the “no-ants’ land” separating their two territories. These peaceful periods are broken up by combats that generally result in a drastic change in territorial boundaries, often the conquest of an entire tree or part of one (e.g., a main branch). The beginning of these combats seems to follow an increase in the population of one of the two belligerent colonies under favorable conditions. For instance, between 1987 and 1990 a colony of *Crematogaster gabonensis* occupied the crown of a large tree in Ndupé, Cameroon. This species is characterized by typical conspicuous polydomous carton nests of different sizes (the largest reaching 1.5 m in height) and very numerous carton shelters where workers attend stictococcids (see details in Taylor 2006). All of the surrounding trees sheltered *Tetramorium aculeatum* or *Oecophylla longinoda* colonies, two other dominant species. The *Crematogaster* colony occupied four trees in 1991 and eight in 1992 at the expense of *Tetramorium aculeatum*. Nevertheless, in 1993 its territory expanded in about six months to 17 trees situated in a square of about 0.5 ha, this time conquering *Oecophylla*-occupied trees (see also Vanderplank 1960 for *Crematogaster* preying on *Oecophylla longinoda*). The population of this *Crematogaster gabonensis* colony was evaluated to be about 5,000,000 workers (confrontation tests between workers were conducted to verify that they really belonged to the same colony). We witnessed this type of colony expansion once: *Crematogaster* workers took over a *Tetramorium*-occupied tree in one day. The workers’ behavior was similar to that of army ants due to their large number and the fact that they formed a column in which individuals were both coming and going, so that new *Crematogaster*

workers were constantly moving to the front of the column. Most of the *Tetramorium* workers and their brood were retrieved (unpublished data).

It seems that when favorable conditions (e.g., habitat) and associations with hemipterans combine to spur the development of a territorial arboreal ant colony, above a certain threshold, workers tend to increase the size of their territories through combats that lead to the destruction of a large part (or all) of a neighboring colony. The subsequent provisioning in proteins permits the victorious colony to become stronger, increasing the probability that it will win further combats. Therefore, territorial variations do not occur progressively, but take place in a series of fits and starts (see also Armbrrecht *et al.* 2001).

THE DYNAMIC OF ANT MOSAICS

Generalities

Because most of the reports on ant mosaics result from snapshot field studies, the longer-term dynamics of the ant mosaic have been neglected. Bigger (1993), however, noted that the ant species changed as cocoa trees aged. Kenne *et al.* (2003) conducted an experimental survey on citrus, guava and mango plantations based around the planned treatment of the trees with insecticides. The insecticide treatments favored ground-nesting, arboreal-foraging ant species such as *Camponotus acvapimensis*, *Myrmecaria opaciventris*, *Paratrechina longicornis* and *Pheidole megacephala*, whereas true arboreal species were recorded on only a few trees. The effect was apparent even two years after the treatments were stopped, illustrating that arboreal-nesting species take over areas slowly. Those trees on plantations that were not treated with insecticides, serving as control groups, sheltered mostly the following arboreal ants: *Tetramorium aculeatum* on guava trees; and *Oecophylla longinoda* on citrus and mango trees, as noted above. The hemipteran species changed in association with changes in the ant species, showing that the ant-hemipteran associations are more important than tree-hemipteran relationships, even if, as suggested by Bigger (1993) the age of the tree can play a role.

The dynamics of arboreal ant mosaics was examined through the ontogenic succession of ants in three Cameroonian tree species (Dejean *et al.* 2007a). *Lophira alata* (Ochnaceae) is a long-lived species that does not furnish any reward to ants, *Anthocleista vogelii* (Gentianaceae) bears extremely well developed EFNs, and *Barteria fistulosa* (Passifloraceae) is a long-lived, EFN-bearing myrmecophyte. A succession of different associated ants according to plant size/age was noted for both *Lophira alata* and *Anthocleista vogelii*: ground-nesting, arboreal-foraging ant species were the first associates, followed by arboreal species that use host tree leaves to build their nests plus some opportunistic species nesting in pre-existing cavities, and then carton-building *Crematogaster* species. A succession was even noted between *Crematogaster* species among the oldest trees. The presence of EFNs on *A. vogelii* slows this process, demonstrating the influence of the plant when a reward is at stake. The comparison with the myrmecophyte *Barteria fistulosa*, which generally remains associated with the same plant-ant species, *Tetraponera aethiops*, during its entire ontogeny, highlights the importance of the selective attractiveness of the trees for their associated ants (see Djiéto-Lordon and Dejean 1999a, 1999b).

Mechanisms involved in the dynamics of an ant mosaic

As for all entities composed of living things, colonies of territorially-dominant arboreal ants begin (foundation), develop, reproduce (swarming), and then die. Although microhabitat conditions and the specific attractiveness of certain tree species *vis-à-vis* certain ant species play a role, two main questions need to be asked.

First, how can an extremely well-established colony disappear? It is known that parasites and predators are frequently concentrated around locally dense host/prey populations. A similar process occurs when territorially-dominant arboreal ant colonies become larger and larger, with the activities of some predators and mostly those of parasites concentrating around them. This was noted on Mexican coffee plantations where a fly parasitizes *Azteca instabilis* ants, disturbing foraging workers, while a coccinellid preys freely on the ants' hemipteran trophobionts, killing them. Fungal pathogens and parasitoid wasps also attack these hemipterans. Given these pressures the hemipteran population decreases, indirectly affecting the dynamic *Azteca instabilis* population, forming clumps of nests whose numbers change from one period to another (Philpott *et al.* 2004; Vandermeer and Perfecto 2006).

While becoming larger and larger African *Oecophylla longinoda* colonies are parasitized by the larvae of several Lycaenid Lepidoptera species; certain of these larvae eat the ants' prey, others eat their brood. Parasitic spiders can also prey on their brood (Collet 1994; see also Pierce *et al.* 2002; Elgar and Allan 2006 for the Australian species *Oecophylla smaragdina*). Bacterial and fungal pathogens can also affect the colonies.

In addition, we saw above that a large colony of territorially-dominant arboreal ant species can be destroyed during combats with a neighboring colony.

Second, how can an incipient colony of a potentially territorially-dominant species inhabit the territory of a very powerful, previously installed colony? In all of the large-scale studies on ant mosaics there are some trees devoid of dominant ants (probably due to the death of a colony), permitting incipient colonies to inhabit the area (and probably to compete with each other). In a Cameroonian mango tree plantation, after insecticide treatments were stopped, we noted the presence of numerous incipient colonies of *Oecophylla longinoda* all nesting in natural cavities of the trees. Some colonies had a single queen, but others had a cluster of up to 34 queens, with several of them producing eggs (Fig. 8). These incipient colonies' minute workers foraged only nocturnally and seemed very timid. After a month the incipient colonies moved to a small, more typical nest built by the first workers. They fold one leaf over on itself and seal it with the silk produced by larvae that they manipulate like shuttles. It seems that the landmarks deposited by the workers are enough to mostly avoid conflicts with the ground-nesting, plant-foraging species previously favored by the insecticide treatments (for landmarks see Hölldobler and Wilson 1990a; Beugnon and Dejean 1992; Dejean *et al.* 2005; see also Offenberger 2007 for *Oecophylla smaragdina*). When the colonies become larger they occupy a large branch and the corresponding bough, limiting the contact zone with alien ants to a small, easily defended area around

the base of the branch. Then, as the colony increases in size it occupies all of the main branches of the tree one after the other and the corresponding foliage; at the end of the process they have occupied the entire tree crown and can easily defend only the upper part of the trunk from the attempts by ground-nesting, plant-foraging ants at incursions.

Later, the *Oecophylla longinoda* were in turn chased away from some trees by *Crematogaster* sp. whose very inconspicuous incipient colonies nest in crevices in the tree bark (see Kenne *et al.* 2003 for the succession of ant species). During an intermediary phase *Crematogaster* workers limit their foraging to the branches themselves and are tolerated by *Oecophylla* that forage mainly at the ends of the twigs and on the leaves. Further studies are needed to understand why the *Crematogaster* workers are tolerated by the *Oecophylla* and how they succeed in completely expelling the *Oecophylla* colonies thereafter.

HOW TO VERIFY THE EXISTENCE OF AN ANT MOSAIC

Sampling techniques

In plantations where trees have low canopies, ant species can be detected visually and counted. Fogging can be used to sample arboreal ants living in the canopies of taller trees (see Floren 2005, Blüthgen and Stork 2007 for a discussion on how fogging data should be used to study mosaics) or several large branches can be cut off from each tree either from the ground using "long-handled saws" (used for oil palm trees) or by climbing up the trees using the single rope technique. Climbers can also beat the vegetation with a stick or spray the bark with natural pyrethrum and collect arboreal ants and suspended soils and search epiphytes for ants. Researchers can easily sample the crowns of trees after they have been felled by farmers or, as is often the case, by local electricity companies to install or protect high-tension wires. Finally, highly specific devices such as cherry pickers, constructions cranes, platforms, towers or manned balloons (e.g. canopy sledge, canopy bubble, canopy glider) can be used to reach the canopies of trees (Basset *et al.* 2003).

As already suggested by Floren (2005) and Blüthgen and Stork (2007) baiting can be especially useful. Indeed, this technique can be used to complement the observation of conspicuous nests located high in the trees, permitting researchers to sample workers for identification to the species level. This also permits them to gather the workers of colonies nesting in hollow branches (such as *Cephalotes atratus* in the Neotropics) without climbing up the trees. Because workers of most territorially-dominant arboreal ant species forage for prey on the ground (see above), baiting is efficacious (used by Dejean *et al.* 2007a on some trees). Baits are placed on the trunks of supporting trees at about 2 m in height where the scout workers of territorially-dominant arboreal species rapidly find them and recruit nest-mates. If competing species also find the baits, they are expelled by the territorially-dominant arboreal species.

The baits can be composed of honey or any sugary substance, and many researchers typically use bits of tuna canned in oil, but even the leftovers of a picnic work. In Cameroon this worked for all tested cases, but in French Guiana *Dolichoderus quadridenticulatus* and *Dolichoderus bidens* workers seemed to be attracted mostly or only to the honey baits (which might be due to the season during which the tests were conducted), and all of these baits also attracted *Wasmannia auropunctata*.

None of these sampling techniques are perfect, but certain of them permit researchers to directly sample ants or to conduct confrontation tests while the results of the others need to be tested using statistical methods. A combination of collection methods allows researchers to obtain a better picture of the entire arboreal assemblage and of the exact spatial distribution of species. Although traps are particularly useful when collecting nocturnal species, sticky traps



Fig. 8 Pleometrosis in *Oecophylla longinoda*. In this species several queens can collaborate to found a new colony (pleometrosis), permitting incipient colonies to grow faster than during haplometrosis, or the foundation by only one queen.

are generally not very effective. By contrast, some arboreal pitfall traps have been tested with success (Kaspari 2000).

Testing the aggressiveness of foraging workers gathered from different trees

Although behavioral assays were standardized in studies dealing with invasive ants (i.e., the interactions between workers were tested; Hollway *et al.* 2002; Le Breton *et al.* 2006), the necessary verification of intercolonial aggressiveness between homo- and/or heterospecific colonies of territorially-dominant arboreal ants is rarely conducted. Nonetheless, Hölldobler and Wilson (1990a: p. 401) verified the intra- and interspecific aggressiveness between *Oecophylla smaragdina* colonies and between the latter and those of *Camponotus* sp. through the reciprocal transportation of workers from one tree to another. Also, inter- and intraspecific aggressiveness between workers was studied in a Cameroonian secondary forest in 1991 using a similar protocol (Dejean *et al.* 1994), permitting the different ant territories to be mapped. In 1993 during the survey using the canopy raft (but not presented in Dejean *et al.* 2000), 10 interaction assays between foraging workers were conducted using a scale going from non-aggressiveness (scored as “1”) to combat with the use of venom (scored as “4”). Fighting was noted in all cases during interspecific confrontations involving *Crematogaster depressa*, *Crematogaster* sp. 1 and *Oecophylla longinoda* (40 tests; scores of 3 or 4). Intraspecific competition was studied each of the five times the canopy raft was positioned, and each time *Crematogaster depressa* occupied the crown of the trees supporting the raft plus the neighboring trees. Workers belonging to the five neighboring trees were confronted and were never aggressive with each other (250 tests, mostly scored as 1, sometimes 2). On the contrary, workers gathered from trees that were more than 300 m apart systematically fought with each other (1000 tests; aggressiveness noted in all cases).

From this approach we can deduce that each colony occupies at least five tree crowns, and probably more. As each tree shelters one to two million workers (Dejean *et al.* 2000), this corresponds to colonies of at least five to 10 million workers. Because workers from distant (> 300 m) nests fight each other, we can deduce that the range of the colonies' territories is an area less than 300 m in radius in this forest where 87.4% of the trees sheltered *Crematogaster depressa* (N = 167). The situation is therefore very different from that of invasive ant species whose workers do not fight during confrontation tests even if they come from areas separated by hundreds of kilometers (Hollway *et al.* 2002; Le Breton *et al.* 2004).

Confrontation tests permit researchers to see if the territories of certain dominant arboreal species are spread over several trees, and to map them. Indeed, territories including adjacent trees have frequently been noted (Room 1971; Majer 1972, 1976a; Hölldobler and Wilson 1990a: p. 401; Dejean *et al.* 1994, see above; Way and Bolton 1997). Also, the territory of co-dominant (sharing the same territory, generally with different rhythms of activity) colonies should be distinguished from the case when the border between two territories passes through the crown of one tree. The two different zones of that crown need to be distinguished for the mosaic to be recognized.

Nevertheless, although these extremely important aggressiveness tests are simple, they are time consuming and so difficult to conduct during snapshot studies.

Statistical analyses of species co-occurrence

When the sampling technique does not permit the limits of the territories of territorially-dominant arboreal species to be established and so the ant mosaic to be mapped, as is often the case in snapshot studies, statistical methods can be used to infer a mutual exclusion between numerically dominant ants and positive associations between them and non-dominant species. These methods and their conditions of

use are reviewed in Blüthgen and Stork (2007). Negative or positive associations between pairs of species can be revealed through *Chi*-square tests based on their combined presence/absence or, more precisely, by measuring the correlation between their abundance on trees.

The null-model analysis of co-occurrence matrices is becoming an increasingly common practice to determine if species co-occurrences are structured rather than random (Floren and Linsenmair 2000; Ribas and Schoereder 2002; Floren and Linsenmair 2005; Sanders *et al.* 2007). The observed data in the matrix (species in rows, sites in columns, presence/absence in cells) are compared by using a co-occurrence index with a “null model” (a randomized matrix derived from the observation). As with any statistical method a critical assessment of the test rationale, power and significance is crucial. For example, depending on the index and the randomization algorithm chosen, a null model analysis is more prone to type I error (i.e. false positive result: failure to detect a random pattern) or type II error (false negative result: failure to detect a non-random pattern) (Gotelli 2000). An illustration of a type II error is the rejection of the ant mosaic hypothesis for our dataset from a secondary Cameroonian forest (Dejean *et al.* 1994) using a null model analysis performed by Ribas and Schoereder (2002). Our dataset is nevertheless a classic example of a totally competitive exclusion between territorially-dominant ants corroborated by additional aggressiveness tests. Ribas and Schoereder (2002) used the C-scored index (Stone and Roberts 1990) with a fixed/fixed randomization algorithm meaning that in all simulated matrices, each species (in rows) will occur with the same frequency and each tree (in columns) will have the same number of species as in the observed matrix. In a situation of total exclusion between individual species (never more than one species per tree), corresponding to an obvious mosaic pattern among territorially-dominant ants, it can be easily demonstrated that this algorithm cannot simulate species co-occurrence patterns different from the observed one (species never co-exist in any simulated matrix exactly as in the observed matrix; trees which did not contain species are never occupied in randomly assembled communities). Despite its use in other studies (Ribas and Schoereder 2004; Floren and Linsenmair 2005; Sanders *et al.* 2007), we therefore recommend not using this randomization algorithm to detect ant mosaics. Depending on whether or not trees can be considered as equally suitable for occupation or not a fixed/equiprobable or a fixed/proportional randomization algorithm (see Gotelli and Entsminger 2004 for details) would be more adequate, but this deserves further investigation.

To test the ant mosaic hypothesis the sampling units should be individual trees (not groups of trees as in our forest edge dataset published in Dejean *et al.* (1994), even though Ribas and Schoereder (2002) also tested the data) or even distinct portions of an individual tree crown when it has been observed that it is split into territories defended by neighboring colonies of competing species. Failure to do so confounds the co-occurrence of territorial species within a single sampling unit with a positive association. Null models may also produce misleading results when the number of positive associations counterbalance or outweigh the number of negative associations (Blüthgen and Stork 2007).

Altogether, as with any statistical tests great care should be taken with the nature of the data analyzed and on the choice of the most appropriate method. One can be confident of the results if the analyses are performed on large datasets and focus on the most frequent ants of the arboreal assemblage (especially if they build large arboreal nests and exploit sugary resources). In any case, ethological studies need to be conducted to better understand cohabitation (see an example in Mercier *et al.* 1998). Furthermore, it should be stressed that, apart from competition, structured patterns of ant distribution may arise from the ways in which ants are associated with resources (Ribas and Schoereder 2002).

TERRITORIALLY-DOMINANT ARBOREAL ANTS AS BIOLOGICAL CONTROL AGENTS

Ants protect their host plants from a variety of arthropod herbivores by preying on them (density-mediated indirect interaction) and through the disturbance or avoidance that they occasion (trait-mediated indirect interaction) (Peacor and Werner 2001; Offenberg *et al.* 2006). For example, when ants are present caterpillars spend less time feeding, resulting in less herbivory on host plants (Rudgers *et al.* 2003). Also chrysomelid females avoid laying eggs on plants when they perceive *Oecophylla smaragdina* landmarks (Offenberg *et al.* 2004); the same is true when lepidopteran females perceive ants or even decoys (ants made of rubber) (Freitas and Oliveira 1996). Consequently, arboreal ants, particularly territorially-dominant arboreal species, can be used as biological control agents.

For centuries *Oecophylla smaragdina* has traditionally been used in southern Asia on citrus tree orchards (Huang and Yang 1987; Way and Khoo 1992; van Mele and Cuc 2000, 2003), and now on Australian cashew trees (Peng *et al.* 1997), while *Oecophylla longinoda* has been useful in controlling fruit flies on mangoes in West Africa (van Mele *et al.* 2007). Furthermore, territorially-dominant African arboreal species protect their supporting trees from a gregarious locust (Dejean 2000), their efficaciousness against defoliators has been noted in coconut, cocoa, and palm tree plantations (Way 1953, 1963; Majer 1976a, 1976b; Bigger 1993; Majer 1993; Dejean *et al.* 1997). The same has been shown in the Neotropics (Majer and Delabie 1993; Vandermeer *et al.* 2002).

Nevertheless, because ants both tend hemipterans and are predatory, their use as pest control agents should be questioned. Because ants protect hemipterans from predators and parasitoids and move them to better feeding sites in exchange for their honeydew, they favor the formation of large hemipteran populations in tree crop plantations. In the same way they can lower the efficaciousness of biological control agents. This affects plant health and fecundity, particularly when hemipterans transmit plant diseases (Way 1963; Hölldobler and Wilson 1990a; Way and Khoo 1992). Nevertheless, these features seem to correspond rather to ground-nesting, arboreal-foraging species rather than territorially-dominant arboreal ants (Kenne *et al.* 2003), something verified in citrus tree orchards in subtropical regions where ground-nesting, arboreal-foraging ants attend large numbers of hemipterans that affect fruit production and tree health. As these ants hunt all kinds of insects, including the predators and the parasitoids of their trophobionts, they should be excluded (Samways 1990; James *et al.* 1999).

On the contrary, in other situations mostly concerning territorially-dominant arboreal ants, those species that attend trophobionts benefit their host plants through a predation rate that outweighs the costs of the hemipteran's consumption of sap (Way and Khoo 1992). In fact, plant fitness increases when hemipterans that do not transmit plant diseases favor ant species that prey or deter other more damaging herbivores (Room 1971; Messina 1981; Philpott and Armbrach 2006).

Consequently, Majer (1976a, 1976b, 1993) introduced the notion of the "manipulation of the ant mosaic". Indeed, the plants support honeydew-producing hemipterans attended by dominant ants, and in return are protected from other herbivores (see also Delabie 2001). In such a context, dominant ants may be effective biological control agents for crop pests, on the condition that the attended hemipterans do not damage the plant. For example, *Tetramorium aculeatum*, *Oecophylla longinoda*, and several species of carton-building *Crematogaster* constitute the base of the mosaic in the canopy of the African cocoa tree plantations. *Crematogaster* spp. tolerate mirids (Heteroptera) and tend Pseudococcidae that transmit diseases to cocoa trees and, thus, should be excluded from any efforts to manipulate the ant mosaic, whereas *O. longinoda* that prey on mirids and tend Stictococcidae that do not cause problems to this plant can be

considered (Majer 1976a, 1976b). The contrary is true for oil palm trees, where *Crematogaster gabonensis* is able to limit attacks by a leaf mining chrysomelid beetle, while *Tetramorium aculeatum* is ineffective and *Oecophylla longinoda* is uncommon (Dejean *et al.* 1997).

Note that if myrmecophytes keep their guest plant-ants from interfering with the work of their pollinators by producing substances repellent to ants on their flowers (Willmer and Stone 1997; Raine *et al.* 2002), this is not the case for non-myrmecophytic plants. For example, *Oecophylla smaragdina* workers reduce the frequency with which pollinators visit their host trees (Tsuiji *et al.* 2004).

CONCLUDING REMARKS WITH INFORMATION ON PLANT-ANTS

It is probable that ant mosaics exist mostly in the Paleotropics due to the presence of truly territorially-dominant arboreal ant species, while in the Neotropics most "dominant" species can share territories with certain others. Also, a certain percentage of territorially-dominant arboreal species is needed to permit the structuring of the territorial mosaic. The statistical analyses of species co-occurrences on trees are a particularly useful tool for snapshot studies when researchers do not know the biology of the ants. Nevertheless, we suggest that only data on numerically dominant species be entered into the analysis in these studies (at least at first) to avoid figuring in the strong "background noise" caused by non-dominant species.

Territorially-dominant arboreal ants, whose territories increase in size in a series of fits and starts, are good predators that have developed strategies permitting them to hunt in a group on the foliage of their host trees. Furthermore, they are able to hunt on the ground around the base of these trees, and to feed on a part of their hemipteran trophobionts, on non-dominant ant species, and even on their enemies after combats.

We saw that the predatory behavior of territorially-dominant arboreal ant species is well adapted to hunting in tree foliage. Workers ambush in a group, they spread-eagle flying insects and then retrieved them whole collectively or cut them up on the spot; depending on the ant species, they can use venom or not. Note that because they limit their activity to their host-myrmecophyte foliage, some plant-ants have evolved even more stunning behaviors. *Azteca shimperi* workers group ambush their prey by placing themselves side-by-side along the underside of a leaf, with just their wide open mandibles visible from the leaf margin. When a prey item lands on the leaf, the vibrations trigger the workers to rush to the prey and seize it, and then spread-eagle it (Fig. 9; unpublished data; see also Morais 1994). *Tetraponera aethiops* workers bore entrances into the hori-



Fig. 9 Associated with the myrmecophyte *Cecropia obtusa*, *Azteca shimperi* workers group ambush by positioning themselves side by side along the leaf margins. They are able to capture large prey thanks to their powerful claws and adhesive pads.



Fig. 10 *Allomerus decemarticulatus* workers build gallery-shaped traps along the twigs of their host myrmecophyte *Hirtella physophora*. Here a grasshopper is captured; note that the extremities of its legs are trapped in the holes of the gallery; workers that hide inside the gallery, under the holes, firmly hold the tips of the prey's appendages.

zontal, hollow branches (domatia) of their host *Barteria fistulosa* near the base of the petiole of the alternate, horizontal leaves. Hidden in the domatia, close to these entrances, they then ambush flying insects. After perceiving the vibrations caused when an insect lands on a leaf, they rush to it, sting it and generally recruit nestmates to spread-eagle it (Dejean *et al.* 2007b). Plant-ants of the genus *Allomerus* collectively ambush prey by building galleries pierced with numerous holes serving as traps. When a prey lands on the gallery each worker waiting in a hole near the landing site seizes an appendage and pulls backward, moving deeper into the trap. With its appendages caught in the trap's different holes, the prey is immobilized and recruited workers sting it repeatedly (**Fig. 10**; Dejean *et al.* 2005). The same behaviors were observed in *Azteca brevis* (see Schmidt 2001; Longino 2007).

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